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On cold hardiness of the egg parasitoid wasp *Telenomus tetratomus* (Thomson, 1861) (Hymenoptera, Scelionidae) – a population regulator of the Siberian moth

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Abstract

Among the factors contributing to the initiation of outbreaks of the Siberian moth, a dangerous pest of the coniferous forests of Northern Eurasia, it is considered important to reduce the regulatory impact of entomophages. One of the most effective regulators of the pest abundance is the egg parasitoid wasp *Telenomus tetratomus* (Thomson, 1861). There is an established opinion that *T. tetratomus* is less cold-resistant than caterpillars of the Siberian moth, and outbreaks of the pest are provoked by cold winters, during which conditions (low temperatures and low snow cover depth) are tolerated by the moth caterpillars but lead to death of the parasitoid. However, the lethal temperature for *T. tetratomus* was determined in an insufficiently controlled experiment more than 60 years ago. We evaluated one of the cold hardiness characteristics of *T. tetratomus*, the supercooling point (*SCP*), which had not been measured previously. Both the host and the parasitoid overwinter in a supercooled state, and freezing is lethal to both. The mean *SCP* of *T. tetratomus* (-21.2±0.2 °C) was found to be 6.3 °C lower than the *SCP* of Siberian moth caterpillars. Comparison of *SCP* distributions and mortality rates at several temperatures allows us to tentatively estimate 50% mortality temperature of the wasp – about -16 °C. The obtained result, analysis of temperatures in the litter of various types of coniferous forests, and published data indicate that the asynchronous mortality of the host and its main parasitoid during wintering, due to differences in cold hardiness, can be considered as the cause of outbreaks of the Siberian moth mass reproduction only with caution.

Keywords
Dendrolimus sibiricus, lower lethal temperatures, supercooling point, surviving, West Siberia

Introduction

The Siberian moth, *Dendrolimus sibiricus* Tschetv., is a well-known dangerous pest of coniferous forests in North Asia. In addition to the Asian part of Russia and Northern Kazakhstan, it is found in North China, Northern Mongolia and on the Korean Peninsula; its larvae infest and defoliate more than 20 species of *Abies*, *Pinus*, *Larix*, *Picea* and *Tsuga* (Gninenko and Orlinskii 2002). In the 20th century, the range expansion of the pest to the west was noted; by the 1950s, this species from the Asian part of Russia had moved into the European part, and is currently found up to 51°E. Moreover, the almost uniform genetics of the continental *D. sibiricus* populations was shown, which suggests its rapid spread to the west of Eurasia (Kononov et al. 2016). Additionally, in recent decades, due to the observed climate change, the pest range has been expanding to the north (Kharuk et al. 2016). Currently, the Siberian moth is listed as a quarantine pest in Annex IAI of Directive 2000/29/EC.

The Siberian moth is characterized by periods of rapid reproduction, leading to a catastrophic increase in numbers (outbreaks) in local areas or on a panzonal scale (taking place in various territories simultaneously) and damage to coniferous forests. Outbreaks are poorly predicted, and opinions differ about the most important triggering and limiting factors for an outbreak. A number of researchers link the dynamics of the pest population with the dynamics of the abundance of entomophages that parasitize on eggs, caterpillars, and chrysalides (Kolomiets 1958, 1961, 1962; Chikidov 2009; Gninenko and Baranchikov 2021). Among approximately 40 species of insect parasitoids that attack Siberian moth (Baranchikov and Montgomery 2014), a special place is given to the egg parasitoid wasp *Telenomus tetratomus* (Thomson, 1861).

Telenomus tetratomus (=*T. gracilis* Mayr., *T. bombus* Mayr. and *T. verticillatus* Kieffer) (Kozlov 1967; Kozlov and Kononova 1983) is widespread in Europe, Russia, Mongolia, China, and Japan. It is considered one of the most effective regulators of pest abundance. The percentage of parasitism is more than 50% at any host abundance and by the end of outbreaks it can reach 100% (Kazansky 1928; Boldaruev 1952; Kolomiets 1962; Kondakov 2002; Baranchikov and Montgomery 2014; Gninenko and Baranchikov 2021). Since the end of the 19th century, *T. tetratomus* has been proposed to control the Siberian moth by breeding and releasing it into the nascent centers of the pest's mass reproduction. There are examples of almost complete elimination of *D. sibiricus* at different phases of foci formation after releasing *T. tetratomus* in them (Vasiliev 1905; Boldaruev 1952; Baranchikov and Montgomery 2014; Gninenko and Baranchikov 2021).

There is a widespread opinion that outbreaks of the Siberian moth are initiated by a decrease or disappearance of the regulatory impact of *T. tetratomus* as a result of its mass death during cold winters with little snow, since the parasitoid is less cold-resistant than its host (Kolomiets 1958, 1961, 1962; Chikidov 2009; Gninenko and

Baranchikov 2021). However, studies on the cold hardiness of the wintering stages of these species, Siberian moth caterpillars and adult *T. tetratomus*, examined different characteristics. For the moth caterpillars, the supercooling point (*SCP*) was determined, and for *T. tetratomus* mortality was evaluated during short-term exposure to some negative temperatures (Kolomiets 1961). At the same time, while *SCP* of the Siberian moth (-14.9±1.5 °C) was studied in the laboratory by the instrumental method (cooling with thermocouples), the temperature limits tolerated by *T. tetratomus* and its mortality rate were determined in the course of an insufficiently controlled half-nature experiment. It is described as follows: *"Several thousand parasitic wasps were placed in a Dewar vessel and stored in natural cooling conditions (between window frames) to determine their frost-resistance. The environmental air temperature was monitored with a minimum thermometer. After exposure to varying degrees of cooling, the parasitic wasps were brought into a warm room for vitalization"* (Kolomiets 1961, p. 119). As can be seen from the above quotation, temperature conditions of the experiment were poorly controlled, and assessment of the wasp survival was approximate, which could significantly distort the true picture of the dependence of mortality on temperature.

Currently, there are two different ideas about lower lethal temperatures of *T. tetratomus*: according to Kolomiyets (1961), the mortality of females begins at -7 ... -9 °C, and already at -9 to -12 °C, 98% of individuals die, while 100% die at -14.7 °C. According to other authors, temperatures below -4 °C are lethal for this species (Baranchikov and Montgomery 2014). Comparison of the above characteristics of cold hardiness of the host and the parasitoid underlies one of the key ideas about population dynamics of the Siberian moth: before the onset of an outbreak, in the wintering sites of both species, there are temperature conditions under which caterpillars survive, while parasitic wasps die due to freezing. Despite the emergence of more accurate laboratory instruments in the 60 years since the experiment of Kolomiets (1961), the study of cold hardiness of *T. tetratomus* has not been refined. Due to the exceptional economic importance of the Siberian moth, its high potential for range expansion and the important role of *T. tetratomus* in regulation of the pest population, biological characteristics of the parasitoid must be carefully studied. Therefore, data on its cold hardiness need to be verified.

We determined the supercooling point of *T. tetratomus*, which had not been studied previously. *SCP* characterizes the ability of organisms to tolerate sub-zero temperatures without the freezing of body fluids. We could not fully assess the second characteristic, the lethal temperature for the survival of the species during long-term exposure, due to a technical failure (at temperatures below -6 °C). Also, the outbreak stopped in areas accessible for the parasitoid collection, which did not allow us to continue the work. However, comparison of the *SCP* values obtained by us and the known levels of mortality at several temperatures (Kolomiets 1961) do not support the idea of insufficient cold hardiness of *T. tetratomus*. Based on the leading role of this species of parasitic wasps in regulating the abundance of the dangerous pest and the possibility of introducing *T. tetratomus* into foci that appear in new territories with climatic conditions other than those in the native range, we considered it necessary to publish the results of our studies to draw the attention of colleagues to the need for a comprehensive study of its biological parameters, including cold hardiness.

Materials and methods

Sampling sites

Siberian moth eggs affected by *T. tetratomus* were collected at the end of August 2018 in one of the sites with high pest abundance (Bakcharsky district of the Tomsk region) on the northeastern spur of the Great Vasyugan mire in the basin of the Gavrilovka River (56.85°N, 82.69°E). In the studied mire, pine-shrub-sphagnum plant communities represent vegetation. The tree stratum is dominated by the stunted *Pinus sylvestris*, up to 4 m high (Fig. 1A), *Pinus sibirica* up to 5 m high is found singly. Projective cover of the grass-shrub stratum (height of 30–40 cm) is 70%; dominants are *Vaccinium uliginosum* (30%) and *Chamaedaphne calyculata* (20%), as well as *Rhododendron tomentosum*, *Andromeda polifolia*, *Rubus chamaemorus*. Among the herbs, *Eriophorum vaginatum* predominates (less than 10%), others are found singly. The basis of the moss-lichen cover is *Sphagnum fuscum* (70%) with an admixture of *Sphagnum divinum*, *Sphagnum angustifolium*, *Sphagnum balticum*, *Polytrichum strictum*, *Pleurozium schreberi*, and *Dicranum polysetum*. Lichens are represented by species of the genera *Usnea* and *Cladonia*.

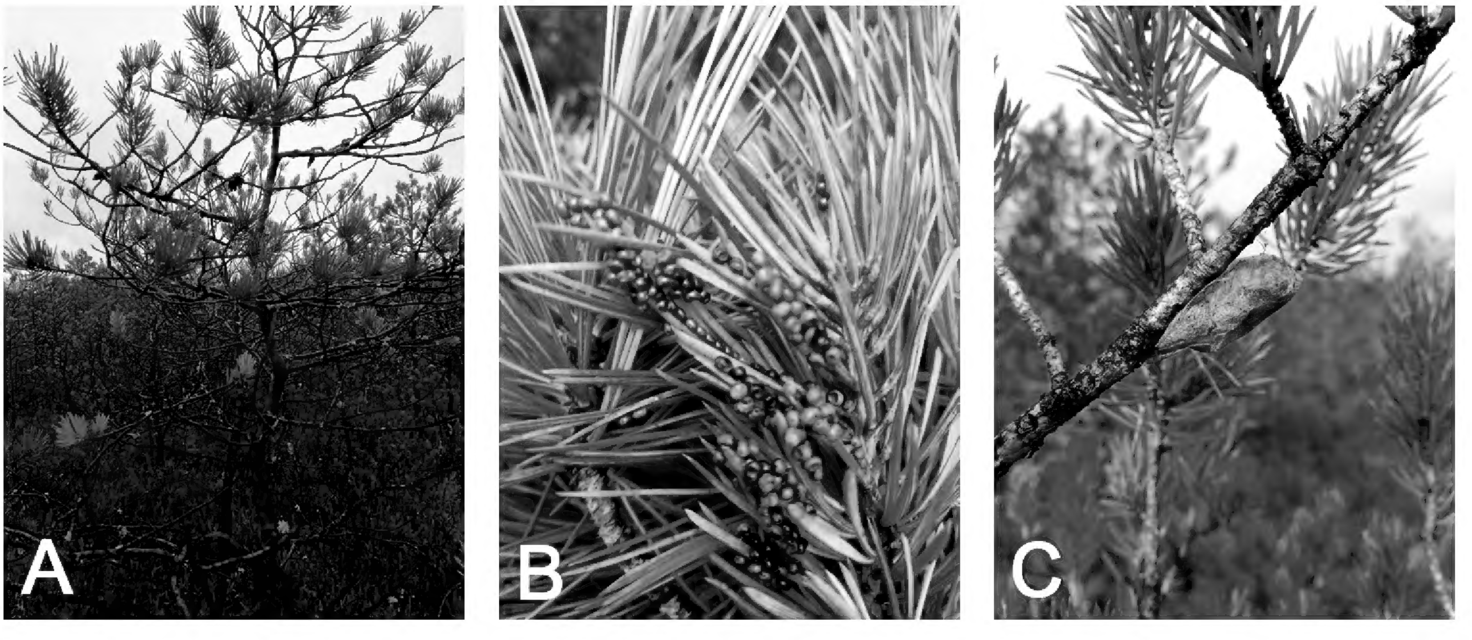

Figure 1. A partially defoliated pines **B** egg-laying and **C** Siberian moth pupal cocoon at the collection site (photo by L. Gashkova).

Animal sampling

Collected shoots (20–30 cm) of *Pinus sibirica* and *P. sylvestris* (Fig. 1B) with Siberian moth egg clutches were packed in non-woven bags or in cardboard boxes, moistened and placed in polyethylene bags, which were stored in the laboratory at temperatures of 15–18 °C. By the time the eggs were collected, most of *T. tetratomus* had already hatched, which was noticeable both by the holes in the eggshells

(Fig. 1B) and by the number of egg parasitoid wasps collected from the shoots in the laboratory. Since only fertilized females of *T. tetratomus* hibernate, in order to minimize the use in experiments of males that die shortly after hatching (Boldaruev 1952; Baranchikov and Montgomery 2014), animals were caught after a week in the laboratory. The dead individuals were not used in experiments. Mobile *T. tetratomus* from needles, bag walls, and Siberian moth eggs were collected with an exhauster and placed 10–20 individuals in 20 or 50 ml test tubes with moist filter paper and a bunch of needles inside. The proportion of eggs damaged by parasitoids was determined using identification keys (Kolomiets 1962). Taxonomic identification of *T. tetratomus* (Kozlov and Kononova 1983; Kononova 2014) was carried out by A.V. Timokhov (Moscow State University, Russia); specimens are deposeitd in Zoological Museum of Lomonosov Moscow State University (ZMMU) (No USNMENT009903625–USNMENT009903629) and in the Biocenology Laboratory of the IBPN FEB RAS (Magadan).

Acclimation and determination of cold hardiness

The egg parasitoid wasps in test tubes were acclimated and cooled in test chambers WT 64/75 (Weiss Umwelttechnik GmbH, Reiskirchen-Lindenstruth, Germany), gradually (at a rate of 1 °C/day) lowering the temperature and keeping at a temperature of 5 °C for a month, 10 days at 1 °C, 20 days at 0 °C, 20 days at -5 °C, and 31–36 days at -6 °C. The temperatures were additionally monitored with preliminarily calibrated temperature loggers (iButton DS1922L, Scientific and Technical Laboratory "ElIn", Moscow, Russia).

The supercooling point (*SCP*) of *T. tetratomus* was assessed approximately 5 months after the individuals were collected and kept in the laboratory at the above temperatures. *SCP* is the temperature at which ice begins to form within the body fluids. Crystallization is accompanied by a surge of heat output and a peak on the temperature diagram. Cooling specimens to *SCP* and then evaluating survival after the rewarming gives an idea of the state, either frozen or supercooled, in which the specimens are able to tolerate freezing temperatures. *SCP* was determined in living specimens stored at -6 °C (n = 73), which, when manipulated, weakly moved their limbs. The standard methodology for *SCP* determination, which has been tested on many invertebrate species, was used (Berman et al. 2010; Berman and Leirikh 2019). The temperature was measured with manganin–constantan thermocouples (wire diameter 0.12 mm). The thermocouple signal was converted using an analog–digital board (ADC LA-TK5) via a DC voltage amplifier and recorded on a computer. The egg parasitoid wasps were fixed on the working junctions of thermocouples with a thin layer of vaseline. The thermocouples with attached insects were cooled in a cooling chamber at a rate of 1 °C/minute. After passing the peak of the freezing onset, the temperatures were lowered by 0.2–7 °C to guarantee freezing of the samples. After that, the wasps were warmed and kept for several hours at 4 °C, then at room temperature, and then the survival was checked.

Winter temperatures in habitats

The temperatures in forest litter in the places where Siberian moth eggs were collected were not determined due to their remoteness. However, they were estimated in typical habitats of the Siberian moth and *T. tetratomus* at a site located approximately 90 km from the egg collection area, in the vicinity of the Podgornoye village (57.79°N, 82.69°E), according to our archival data. In 2008–2009, in this area, a large-scale study of temperatures in soils and forest litter was carried out in various biotopes, including several types of coniferous forests: at a pine-shrub-sphagnum bog (similar to the one at which Siberian moth eggs with egg parasitoid wasps were collected); in a mature dark coniferous (cedar and fir) forest with high crown density on a river side of the Iksa River; in plantations of pine and in a narrow snow-protective spruce-pine belt. The temperature loggers (DS1922L) recorded temperature 6 times a day in typical *T. tetratomus* wintering places, forest litter or moss cover at three depths: at the surface (0–2 cm) and at 10 or 20 cm (depending on the cover thickness). Data on air temperatures and snow depth were obtained at the meteorological station in the Podgornoe village, located no more than 7 km from the places where the temperature loggers were positioned and at the meteorological station in the Bakchar village, located about 40 km from the place where the animals were collected for experiments.

Results

Observations in nature

At the end of August, pupal cocoons and eggs of the Siberian moth were found on trees in the studied bog (Fig. 1B, C). Among the several hundred collected eggs examined in the laboratory, no more than 3% had signs of caterpillars emerging (brownish color of the shells, a large irregularly shaped hole with uneven edges). The vast majority of eggs had traces of parasitoids in them, among which *T. tetratomus* predominated (gray shells, one hole of small diameter with smooth edges, see Fig. 1B). In the summer of 2019, during an inspection of this territoty, as well as forests damaged by the Siberian moth in the Chainsky and Tomsk regions, caterpillars, butterflies or eggs of the moths were not found, i.e., the year of the Siberian moth egg collection (2018) was the last year of the three-year pest outbreak.

Cold hardiness of *Telenomus tetratomus*

The majority of *T. tetratomus* (85% of the sample) cooled in the laboratory to -6 °C survived: when they were transferred to positive temperatures, they began to move after a few minutes. *SCP* values ranged from -15.7 to -26.2 °C, with an average of -21.2±0.2 °C (Fig. 2). None of the animals cooled by another 0.2–7 °C after reaching *SCP*, including those that spent only a few seconds in the frozen state, survived after a long period at positive temperatures.

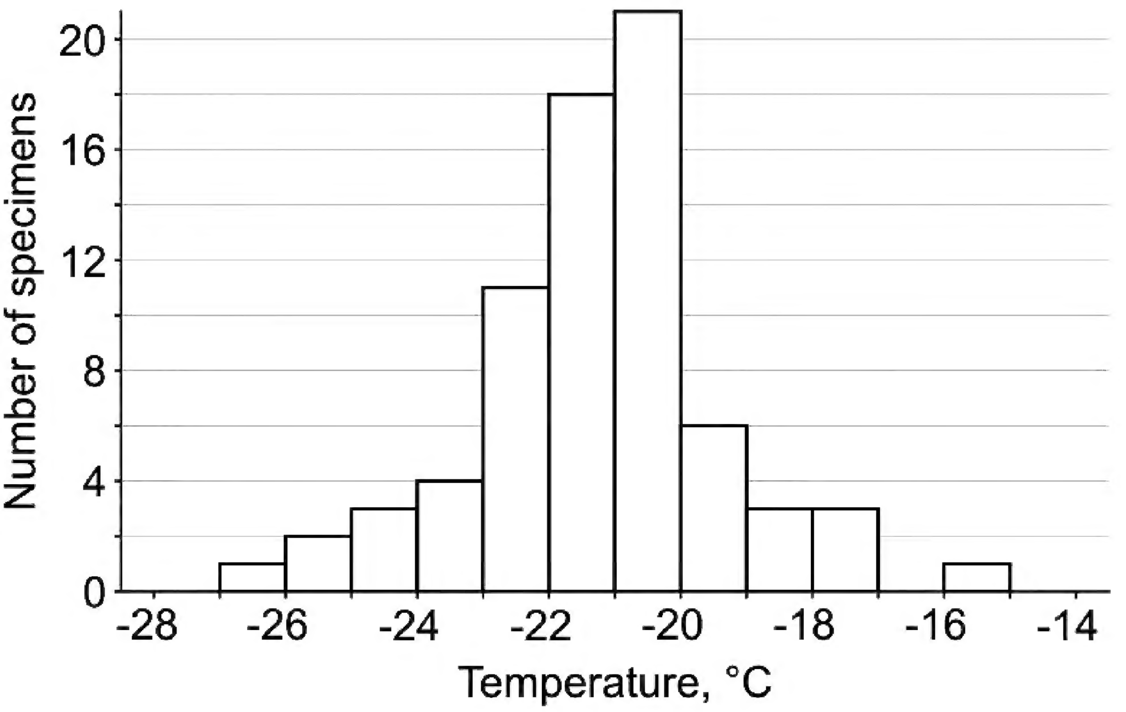

Figure 2. Histogram of *Telenomus tetratomus SCP* distribution.

Minimum temperatures in winter habitats of *Telenomus tetratomus*

In the winter preceding the time of collecting Siberian moth eggs (2017–2018), the minimum air temperature was -40.9 °C, and the maximum snow depth was 73 cm (according to data from the meteorological station in the Bakchar village). In the area of soil temperature measurements (surrounding the Podgornoe village), the minimum air temperature was the same (-41 °C), with a slightly lower snow cover depth (69 cm). Under these conditions, the minimum temperature in the ground cover in different types of coniferous forests varied greatly. In the upper 2 cm of the litter, it was the lowest (-25 °C) in the pine-shrub-sphagnum bog with sparse low-growing pines and cedars and in the mature dark coniferous forest with high crown density on the river side (-15 °C). However, in the plantations of pine and in the narrow snow-protective spruce-pine belt, the temperatures were much higher (-7 and -9.5 °C, respectively). At a depth of 10 cm in the litter in both areas of pine plantations, the minimum temperatures were 1–2.5 °C higher than at the surface (-6.2 and -7 °C), respectively. In the litter in the dark coniferous forest, even at a depth of 10 cm, temperatures dropped to -12.8 °C. It was also cold on the raised bog in the depths of the thick and loose moss-grass-shrub cover – temperatures of -7 °C were recorded no closer than 20 cm from the surface.

Discussion

Coniferous forests in the Tomsk region periodically suffer from outbreaks of the Siberian moth, the last of which was observed in 2016–2018. This outbreak was part of a panzonal outbreak that engulfed many regions of Asian Russia. In the year of our research, the outbreak in the Tomsk region was in the eruptive phase. However, in 2019, the number of Siberian moths decreased sharply and the vast majority of the local

outbreaks disappeared. According to forest pathologists, this was facilitated by a high level of parasitoid infection of eggs, caterpillars and chrysalides in 2018 and weather conditions in 2019. In most of the region's territories, as in our studies, more than 90% of Siberian moth eggs were infested with parasitoids, of which the most common was *T. tetratomus* (Denisova et al. 2020). These observations once again confirm the significant role of parasitoids in regulating the abundance of the Siberian moth.

We have estimated the supercooling point of *T. tetratomus* for the first time. The significant survival rate of *T. tetratomus*, which were at negative temperatures for about 2 months (down to -6 °C), and 100% death after freezing on thermocouples (i.e. at temperatures below *SCP*) indicate that they are not freeze-resistant, and therefore are only able to overwinter in a supercooled state, like many other hymenopteran parasitoids (Carrillo et al. 2005; Hanson et al. 2013; Santacruz et al. 2017). The real ecological value of *SCP* for freeze intolerant species is ambiguous. Though *SCP* is often criticized as a poor indicator of cold hardiness, it is used in many studies because it provides crucial information on the lower lethal temperature of freeze intolerant species of non-tropical invertebrates and constitutes a convenient comparative index (Bale 1987; Renault et al. 2002). Together with the lower lethal temperatures, it gives an idea of cold hardiness of a species that can be obtained from laboratory studies.

Our average *T. tetratomus SCP* values (-21.2±0.2 °C) were found to be 6.3 °C lower than the average moth caterpillar *SCP* values (-14.9±1.5 °C) (Kolomiets 1961). Such a large difference in the average *SCP* of these species living together and hibernating in a supercooled state casts doubt on the established opinion about the greater cold hardiness of the Siberian moth compared to the parasitoid.

The statistical distribution of *T. tetratomus SCP* (Fig. 2) and *SCP* cumulative curve (Fig. 3) have shapes typical of many small invertebrate species studied, including Hymenoptera (Block 1982; Berman et al. 2010; Berman and Leirikh 2019). However, the construction of the *T. tetratomus* cumulative mortality curve according to Kolomiets (1961) and its comparison with the cumulative *SCP* curve that we obtained raise a number of questions (Fig. 3).

First, none of the more than 20 species of invertebrates that we have previously studied wintering in a supercooled state are characterized by such a narrow (only 3 °C) diapason of lethal temperatures. Such examples from the literature are also unknown to us. In the experiments of Kolomiets (1961), *T. tetratomus* females only began to die at -9 °C, and when it reached -12 °C, already 98% of individuals from a sample of several thousand animals were dead. Indeed, the death of the least prepared individuals for wintering in different species usually occurs at slightly subzero temperatures (-3 ... -5 °C); as temperatures decrease, mortality increases, and the most cold-resistant individuals die at temperatures close to the minimum *SCP* (Berman et al. 2010; Santacruz et al. 2017; Berman and Leirikh 2019). Thus, death occurs in a large temperature interval, significantly greater than 3 °C (from negative near zero temperatures to those comparable to minimum *SCP* values). Usually, this interval reaches 10–25 °C (Fig. 4).

Second, the temperature of 100% mortality of *T. tetratomus* (-14.7 °C) revealed by Kolomiyets (1961) was found to be higher than the results of our experiments, with the *SCP* of the least cold-resistant individual at -15.7 °C (Fig. 3). This situation is not

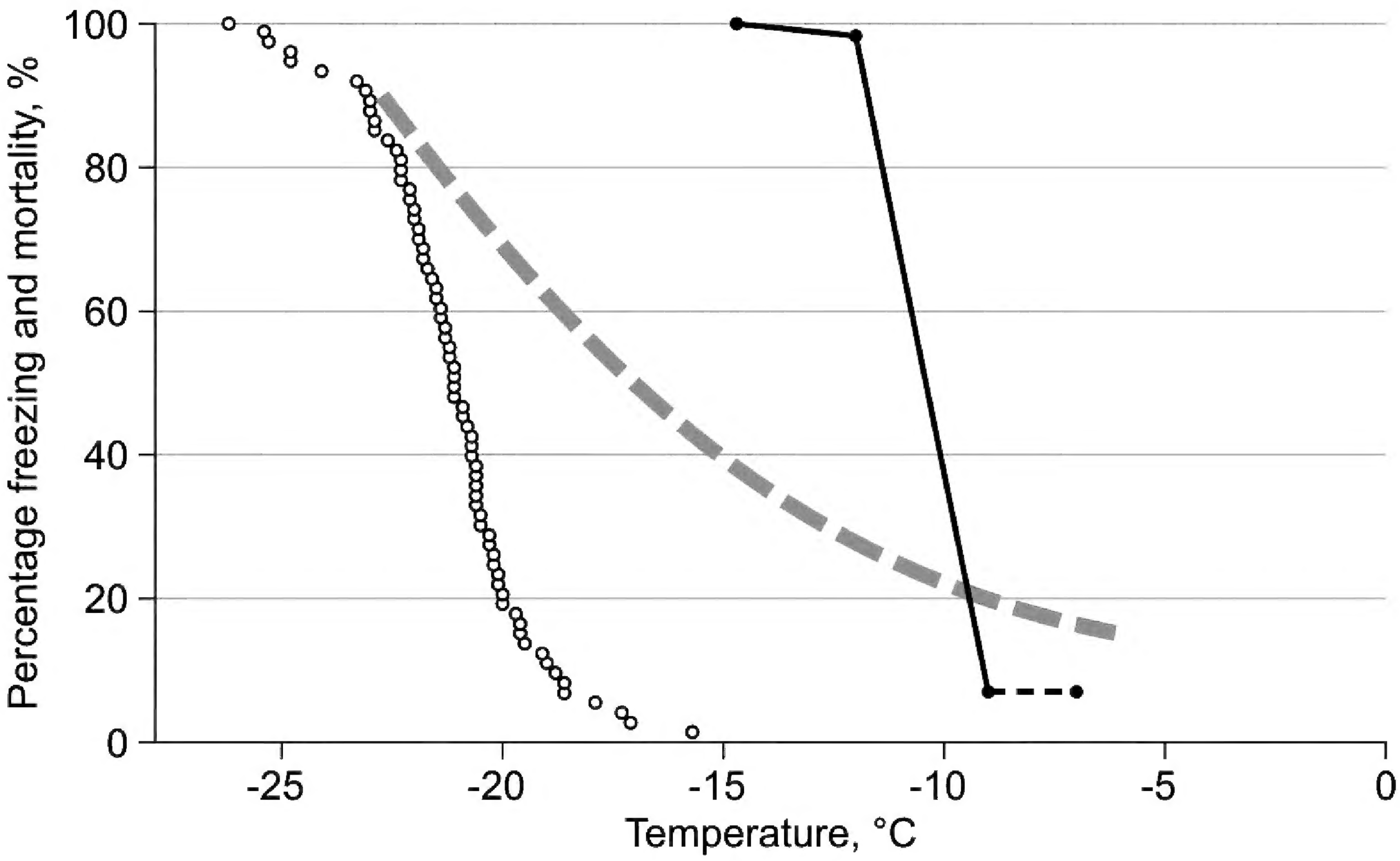

Figure 3. Cumulative values of supercooling points and mortality at negative temperatures of *Telenomus tetratomus*. The black line is the mortality at different temperatures (according to: Kolomiets 1961), open circles indicate the *SCP* obtained in our experiments, the gray dashed line indicates our predicted mortality.

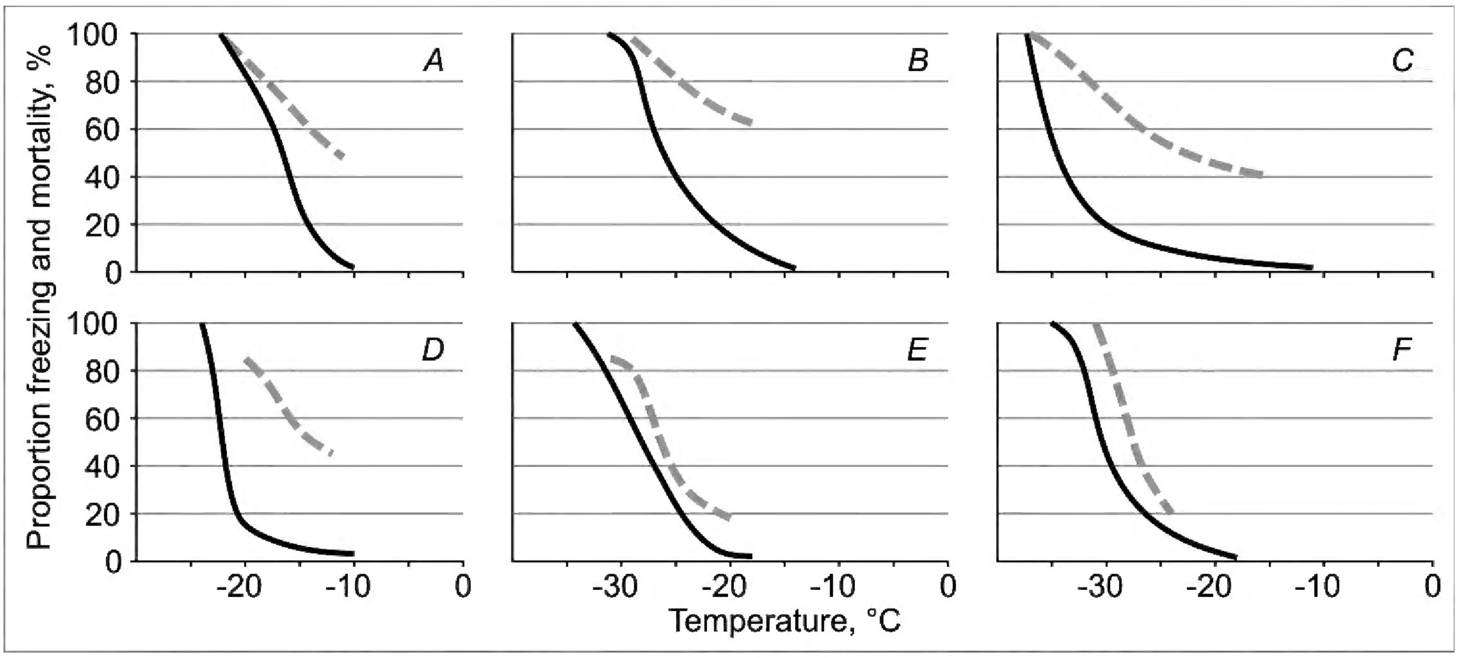

Figure 4. Cold hardiness characteristics of several ant species (plotted according to: Berman et al. 2010, Berman and Leirikh 2019). Black lines indciate *SCP* cumulative curves, gray dashed lines indicate cumulative mortality curves upon exposure to the indicated temperatures for 1 day **A** *Formica sanquinea* **B** *Myrmica angulinodis* **C** *Camponotus herculeanus* **D** *Formica execta* **E** *Myrmica kamtschatica* **F** *Formica gagatoides*.

typical for species living in temperate seasonally cold latitudes and is probably typical only for tropical species (Renault 2002).

Third, the curves of the cumulative *SCP* and cumulative mortality turned out to be almost parallel and separated from each other by 10–11 °C throughout the entire length

(Fig. 3). An analysis of literature data and our results of studying the cold hardiness of various groups of invertebrates in temperate latitudes wintering in a supercooled state (ants, beetles, butterflies, mollusks, etc.) suggests that such a disposition between the mortality curve and the *SCP* curve is an atypical situation (Berman et al. 2010; Berman and Leirikh 2019). In the vast majority of species, these two curves converge strongly with decreasing temperature, as, for example, in ants (Fig. 4A–D). Examples of parallel arrangement of the two curves are less common. At the same time, the curves of mortality and *SCP* in such cases are separated from each other by no more than 2–3 °C (Fig. 4E, F).

Considering all of the above, we can conclude that the high (more than 90%) mortality of *T. tetratomus* in the temperature interval from -9 to -12 °C is most likely the result of an incorrect conduction of the experiment and the lack of proper control of the temperatures at which the insects were held. Using a graphical method, 50% mortality temperature for *T. tetratomus* can be estimated at about -16 °C (Fig. 3), which is at least 5 °C lower than indicated by Kolomiyets (1961) and more than 10 °C lower than indicated by Baranchikov and Montgomery (2014).

For a number of invertebrates, including Hymenoptera, geographical variation in cold hardiness due to climatic differences has been shown: the average *SCP* of individuals in southern populations (with higher temperature) is higher than in northern ones (Block 1982; Turnock and Fields 2005; Santacruz et al. 2017). However, an analysis of temperatures in the wintering places of *T. tetratomus* (in the litter of coniferous forests) showed that, despite the more southerly position of the Tuvan population (52°N), which was studied by Kolomiets (1961), compared to the one studied by us, the temperatures in the wintering places of the parasitoid in Tuva are lower. In a coniferous forest, in the litter and under the moss cover at a depth of almost 20 cm, Kolomiets (1961) estimated the minimum temperatures as -18 °C due to the thin snow layer (20–22 cm) and low air temperatures (down to -48 °C). In the habitats that we studied, even at half the depth in the litter (10 cm), the minimum temperatures were higher (from -6.2 °C to -12.8 °C). The winter in which we measured the temperatures was slightly colder than usual and the minimum temperature reached -41 °C (against an average of -39.5 °C for the last 10 years) and with a slightly lower snow depth (69 cm against 73 cm on average for the last 10 years). So, it can be assumed that the forest litter was somewhat colder than usual. But even in relatively cold winters, the temperatures in the litter turned out to be higher than in the studied Tuva habitats. Thus, the comparison of winter temperature conditions in the wintering sites of *T. tetratomus* does not confirm the climatic conditionality of the obtained differences in cold hardiness of this species.

Conclusions

Our study of cold hardiness of *T. tetratomus* and the analysis of temperatures in the places of its overwintering indicate that the causes of Siberian moth outbreaks need further study. Both the host and its parasitoid overwinter in a supercooled state, and freezing is lethal to both. The average *T. tetratomus SCP* values (-21.2±0.2 °C) turned out to

be 6.3 °C lower than the average Siberian moth caterpillar *SCP* values (-14.9±1.5 °C) obtained in the experiments by Kolomiets (1961). Such a large difference in average *SCP* casts doubt on two well-established positions: firstly, about the greater cold hardiness of the Siberian moth compared to its parasitoid; secondly, that one of the main reasons for the beginning of an increase in number of the Siberian moth is the death of *T. tetratomus* population during cold winters with little snow, while the host safely overwinters (Kolomiets 1961, 1962; Chikidov 2009).

The analysis of *SCP* distribution and *T. tetratomus* mortality allows concluding that 50% mortality temperature can be estimated at about 5 °C lower than indicated by Kolomiets (1961) and more than 10 °C lower than indicated by Baranchikov and Montgomery (2014), at about16 °C. The presented results undoubtedly require determination of *T. tetratomus* mortality at several temperatures with simultaneous *SCP* measurements. We hope that the present research will stimulate colleagues to conduct a full-scale study of cold hardiness of *T. tetratomus* and other parasitoids, which will provide an adequate understanding of the possible ways of regulating the Siberian moth abundance not only within the existing range, but also with its possible expansion into Europe, and the prospects for introduction of parasitoids into cold regions.

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References

Bale JS (1987) Insect cold hardiness: freezing and supercooling – an ecophysiological perspective. Journal of Insect Physiology 33(12): 899–908. https://doi.org/10.1016/0022-1910(87)90001-1

Baranchikov YN, Montgomery ME (2014) Siberian Moth *Dendrolimus sibiricus* (Chetverikov) (Lepidoptera: Lasiocampidae). In: Van Driesche R, Reardon RC (Eds) The use of classical biological control to preserve forests in North America. United States Department of Agriculture, Forest Service, Forest Health Technology Enterprise Team: 393–391.

Berman DI, Alfimov AV, Zhigulskaya ZA, Leirikh AN (2010) Overwintering and cold-hardiness of ants in the Northeast of Asia. Pensoft Publishers, Moscow-Sofia, 294 pp.

Berman DI, Leirikh AN (2019) Overwintering and cold hardiness of the invertebrates in the Northeast Asia. KMK Scientific Press Ltd., Moscow, 314 pp. [In Russian]

Block W (1982) Supercooling points of insects and mites on the Antarctic Peninsula. Ecological Entomology 7(1): 1–8. https://doi.org/10.1111/j.1365-2311.1982.tb00638.x

Boldaruev VO (1952) Siberian moth parasites in Eastern Siberia. Entomologicheskoe Obozrenie 32(1): 56–68. [In Russian]

Carrillo MA, Heimpel GE, Moon RD, Cannon CA, Hutchison WD (2005) Cold hardiness of *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae), a parasitoid of pyralid moths. Journal of Insect Physiology 51: 759–768. https://doi.org/10.1016/j.jinsphys.2005.03.006

Chikidov II (2009) The role of climatic factors in mass reproduction of Siberian silkworm in Central Yakutia in 1998–2001. Vestnik Yakutskogo gosudarstvennogo universiteta 6(3): 8–12. [In Russian]

Denisova NB, Sobolev AA, Shipinskaya US (2020) Study results of Siberian moth (*Dendrolimus sibiricus* Tschetw.) outbreak foci in Vasyugan forestry of Tomsk region. Lesnoy vestnik 24(6): 65–72. [In Russian] https://doi.org/10.18698/2542-1468-2020-6-65-72

EU (2000) Council Directive 2000/29/EC of 8 May 2000 on protective measures against the introduction into the Community of organisms harmful to plants or plant products and against their spread within the Community. Official Journal of the European Communities 169: 1–112.

Gninenko YI, Baranchikov YN (2021) Factors of biological regulation of Siberian moth populations and their use for forest protection. Sibirskiy Lesnoy Zhurnal 5: 9–25. [In Russian] https://doi.org/10.15372/SJFS20210503

Gninenko YI, Orlinskii AD (2002) *Dendrolimus sibiricus* in the coniferous forests of European Russia at the beginning of the twenty-first century. EPPO Bulletin 32(3): 481–483. https://doi.org/10.1046/j.1365-2338.2002.00593.x

Hanson AA, Venette RC, Lelito JP (2013) Cold tolerance of Chinese emerald ash borer parasitoids: *Spathius agrili* Yang (Hymenoptera: Braconidae), *Tetrastichus planipennisi* Yang (Hymenoptera: Eulophidae), and *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae). Biological Control 67: 516–529. https://doi.org/10.1016/j.biocontrol.2013.08.015

Kazansky KA (1928) Siberian pine moth as a pest in the forests of the Buryat-Mongolian Republic. Zashchita rasteniy ot vrediteley 4: 10–12. [In Russian]

Kharuk VI, Im ST, Yagunov MN (2018) Migration of the northern boundary of the Siberian silk moth. Contemporary Problems of Ecology 25(1): 32–44. https://doi.org/10.1134/S1995425518010055

Kolomiets NG (1958) Parasites of pests of forest insects in Siberia. Entomologicheskoe Obozrenie 37(3): 603–615. [In Russian]

Kolomiets NG (1961) Cold resistance of Siberian mot caterpillars and temperature regime in their wintering places. Izvestiya SB AN USSR 1: 113–120. [In Russian]

Kolomiets NG (1962) Parasites and predators of the Siberian moth. SB AN USSR Academy Scientific Publisher, Novosibirsk, 173 pp. [In Russian]

Kondakov YP (2002) Mass breeding of the Siberian moth in the forests of Krasnoyarsk Territory. Entomologicheskie issledovaniya v Sibiri 2: 25–74. [In Russian]

Kononov A, Ustyantsev K, Wang B, Mastro VC, Fet V, Blinov A, Baranchikov Y (2016) Genetic diversity among eight *Dendrolimus* species in Eurasia (Lepidoptera: Lasiocampidae) inferred from mitochondrial COI and COII, and nuclear ITS2 markers. BMC Genetics 17: 173–182. https://doi.org/10.1186/s12863-016-0463-5

Kononova SV (2014) Telenominae of the Palaearctics (Hymenoptera, Scelionidae). Subfamily Telenominae. Naukova Dumka, Kiev, 487 pp. [In Russian]

Kozlov MA (1967) Palaearctic species of egg parasites of the genus *Telenomus* Haliday (Hymenoptera, Scelionidae, Telenominae). Entomologicheskoe Obozrenie 46: 361–378. [In Russian]

Kozlov MA, Kononova SV (1983) Telenominae of the fauna of the USSR (Hymenoptera, Scelionidae, Telenominae). Nauka, Leningrad, 336 pp. [In Russian]

Renault D, Salin C, Vannier G, Vernon P (2002) Survival at low temperatures in insects: what is the ecological significance of the supercooling point? CryoLetters 23(4): 217–228.

Santacruz EN, Venette R, Dieckhoff C, Hoelmer K, Koch RL (2017) Cold tolerance of *Trissolcus japonicus* and *T. cultratus*, potential biological control agents of *Halyomorpha halys*, the brown marmorated stink bug. Biological Control 107: 11–20. https://doi.org/10.1016/j.biocontrol.2017.01.004

Turnock WJ, Fields PG (2005) Winter climates and cold hardiness in terrestrial insects. European Journal of Entomology 102(4): 561–576. https://doi.org/10.14411/eje.2005.081

Vasiliev IV (1905) Pine (*Dendrolimus pini* L.) and cedar (*Dendrolimus segregatus* Butl.) moths, their lifestyle, harmful activities and ways to control them. Trudy buro po entomologii 5(7): 1–102. [In Russian]